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Population studies on *Folsomia octoculata* (Collembola : Isotomidae) in a subalpine coniferous forest

BY

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I. — INTRODUCTION

Population studies on collembolan species under natural conditions are scarce except those on phenology and distribution in given areas. The few studies so far reported on the field biology of collembolan populations have some defects, especially in ways to measure the body length and to evaluate defects in extractions passed through Tullgren funnels, which give decisive effects on the population estimation.

In previous papers (TAMURA, 1974; 1976), these defects have mostly been solved by means of relatively simple improvements. These improved techniques will be adopted to the study of a natural population of Collembola.

Fortunately I had an opportunity to survey the collembolan fauna at Mt. Shigayama for four years (1968-1971) as a member of the JIBP-PT group. In the course of studying the faunal makeup, phenology and micro-distribution, it was noted that conspicuously large-sized individuals of *Folsomia octoculata* were obtained there, though few in number, together with individuals of sizes commonly observed in other localities at lower altitudes (cf. NIIJIMA, 1971; TAKEDA, 1973). These large individuals were assumed to be overgrown individuals produced by the prolongation of life span due to the low temperatures prevailing in this montane climate. Under such circumstance, individuals of the population as a whole must show a more gradual growth in body size. If such is the case, it is very convenient for population study, because even a survey with long sampling intervals may permit determination of the individual growth and other population characteristics.

In addition, this species was always dominant in quantity there as noted

later. Therefore, this local population was chosen as the subject of study to analyse its population dynamics and life history under natural conditions by adopting the improved techniques previously reported (TAMURA, 1974; 1976) as a primary step to obtain a « real » ecology on various species in other localities hereafter.

A taxonomic study on collembolan species in the area concerned has already been published by YOSII (1969). Other information concerning the phenology and micro-distribution of Collembola in this area will be reported elsewhere.

II. — AREA SURVEYED

The area surveyed, Otanomosu-no-Taira * is situated in the subalpine coniferous forest about 1,800 m in altitude, on the northeastward plateau of Mt. Shigayama located in Shiga Heights, Nagano Pref., central Japan. The forest is dominated by *Tsuga diversifolia* Masters and *Abies mariesii* Masters, with some admixture of deciduous trees, *Betula Ermani* Chamisso, etc. The forest

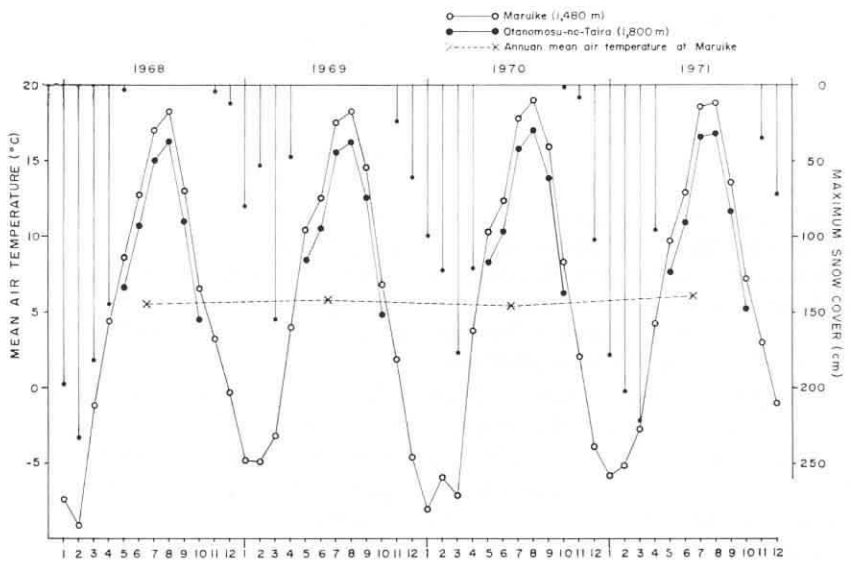

FIG. 1. — Monthly mean air temperature and maximum snow cover during four years surveyed (1968-1971) in Shiga Heights, with estimated data at Otanomosu-no-Taira.

floor is patchily covered with *Sasa sp.* There are numerous mounds of soil (1-3 m in height, 5-10 m in bottom diameter) with thick litter layer all over the area, so the forest floor is complicated by irregular successions of mounds and depressions. The main soil types of the area are wet podsol at the feet of mounds and in depressions, dry podsol on the tops of mounds, and brown forest soil at the limited places where the deciduous trees grow.

* The Shigayama IIBP area.

Generally the annual mean air temperature is about 3-4° C and there is a heavy accumulation of snow during about half a year from the beginning of November to the end of next May, the deepest snow being about 3 m in height in February. Precipitation is heavy, and the area gloomy even in the daytime as little sunlight passes through the canopy. Therefore the soil is cool with a high water content throughout the year. Fig. 1 shows the climatic condition during the four years (1968-1971) when the survey was carried out, observed at Maruike (1,480 m alt.) about 1.5 km from the study area (by the courtesy of the Nagano Office of Japan Weather Association). Further, an estimate of the air temperature at the study area during the season without snowcover is added, based on the altitudinal difference between both places and adopting 0.6° C decrease for every 100 m elevation. The seasonal fluctuation of monthly mean air temperature at Otanomosu-no-Taira was annually very similar during the four years. But the summers in 1970 and 1971 were somewhat warmer than in other years. Depth of snow cover was also annually very similar except for the beginning of 1969. Annual mean air temperature, mean air temperature during growth period (mid-May - mid-October), number of days beyond 5° C and the warmth index, or month-degree (KIRA, 1945, after IMADATÉ, 1973) are summarized in Table 1.

TABLE I

Climatic data at Otanomosu-no-Taira during the four years (1968-1971)

Year	Annual mean air temp. (°C)	Mean air temp. (°C) during growth period	Days beyond 5° C	Warmth index (°C month)
1968	3.5	10.7	155	33.0
1969	3.8	11.3	165	35.5
1970	3.4	11.9	170	38.7
1971	4.1	11.4	165	37.4
Mean	3.7	11.3	164	36.2

III. — SPECIES STUDIED

A faunistic study on the collembolan assemblage in the present area in 1969 showed that at least 48 species occurred there, among which *Folsomia octoculata* Handschin was overhelmingly dominant throughout the year, making up always about 30-40 % of the total collembolan (TAMURA et *al.*, unpublished). Accordingly, *Folsomia octoculata* was selected as the representative of collembolan populations at Otanomosu-no-Taira.

F. octoculata was originally described by Handschin, from Java, in 1925. In 1939, Yosii gave the first record of this species in Japan. Thereafter several records were presented from various localities in Japan: Hidaka-Mombetsu, Hokkaido (TAMURA et *al.*, 1969); Mt. Sobo, Kyushu (TANAKA, 1970 a); Asakawa, Tokyo (NIIJIMA, 1971, '75); Kamigamo, Kyoto (TAKEDA, 1973); and Kushiro, Hokkaido (UCHIDA & SUMA, 1973). Except at Hidaka-Mombetsu, the local collembolan faunas were mostly dominated by this species. Further this species was also reported

from Singapore and Malaya (Yosii, 1959), Pakistan (Yosii, 1963), Nepal (Yosii, 1966) and Korea (Lee, 1974). Uchida (1957) has suggested a wide distribution all over Japan for this species. Probably the species is distributed throughout an extensive zone from Indonesia to northern Japan. But no material has been recorded from North America and Europe where intensive studies on Collembola have been performed for long time.

IV. — METHOD

Five sampling sites were selected at the sections of wet-podsol soil without *Sasa*. These were more than 20 m apart from each other, and mostly coincided with depressions of the forest floor. As shown in the calendar given below, sampling was carried out irregularly for four years from June in 1968 to December in 1971, usually during the hours from 10:00 to 12:00.

Sampling dates		Remarks
June 22	1968	
August 27		
October 20		
June 13	1969	
July 18		
August 19		
September 17		
October 22		with snow cover 3 cm deep
November 3		with patchy snow cover
May 25	1970	
July 22		
September 12		
November 17		with snow cover 5 cm deep
July 7	1971	
September 20		
November 18		with snow cover 30 cm deep
December 14		with snow cover 140 cm deep.

Soil samples (5 cm long, 4 cm wide and 5 cm deep) were taken from three different depths at each site every time as follows: 5 samples from 0-5 cm including surface litter, 2 from 5-10 cm and 1 from 10-15 cm, summed up to 40 samples each time (for details see Aoki, 1963; Kikuzawa et *al.*, 1968). Each sample was separately put into a polyethylene bag and brought to the laboratory, which is situated nearly at 1,500 m alt. The animals were extracted from soil samples with slightly modified Tullgren funnels with 40 W electric bulbs as heat source which were run for 42 hours (for details see Kikuzawa et *al.*, 1968; Niijima, 1971), kept in vials filled with 70 % alcohol, and transported to my laboratory in Mito for subsequent treatment.

At first the extracted materials were poured into a petri dish from which the larger animals such as Oligochaeta, Chilopoda, Diplopoda, Coleoptera, etc. were removed to give a clear view of the smaller fauna. The remaining animals, mainly Collembola and Acarina, were mounted all together in total preparations (Tamura, 1974) with Neo-Shigaral solution for the samples taken in 1968 and with Hoyer's solution for the samples in 1969-1971. All preparations were laft alone till the mounting media hardened sufficiently, at least for more than a month. Prior to the following examinations, the effects of both mounting media on the body length of *F. octoculata* were studied to determine the natural body length. The hardened preparations were placed on the stage of a profile projector in order to count the individual number of *F. octoculata*. Then drawings of the body length were also prepared for every individual for measurement of the body size using the profile projector-curvimeter method (Tamura, 1974). All values for body length were corrected to remove the effects of the mounting media. The corrected data were lumped up at intervals of 0.1 mm for 1968- and 1969-samples and at intervals of 0.05 mm for 1970- and 1971-samples, for in the latter case the technical refinement for the profile projector-curvimeter method was advanced by the experience gained in the

former case. For every sampling time all data were arranged into the size class composition of the population passed through Tullgren funnels. The number of individuals of each size class was corrected by the correction equation (TAMURA, 1976), then the « natural population » was given for each sampling time. In these calculations, the equations were seasonally assigned as follows: the November equation for the seasons with snow-cover during November to May; and the August equation for the snowfree seasons from June to October (cf. TAMURA, 1976).

V. — RESULTS

A. Effects of mounting media on the body length.

At first 110 individuals of *F. octoculata* were selected, including every size from minimum to maximum. The specimens were individually picked up with a micropipette and transferred to a petri dish containing 70 % alcohol on the stage of a profile projector, and then the line drawing of body length was traced on a sheet of thin paper. The materials treated were mounted with Neo-Shigaral solution in a microscopic preparation in a group of five or six individuals, arranging them in the order of previous measurements. Next, 52 individuals were selected for the treatment with Hoyer's solution. The body lengths were drawn and the microscopic preparations were made, following the procedure mentioned above. After hardening of the medium, line drawings were made of the body lengths of all individuals in the preparations. The line drawings were measured for their lengths at intervals of 0.01 mm by means of the profile projector-curvimeter method (TAMURA, 1974).

Every set of the data of body lengths before and after mounting was plotted in Figs. 2 and 3 for Neo-Shigaral and Hoyer's solutions, separately. When a point lies on the left of the equivalent line, then it means that the body shrank after mounting, and when it lies on the right, this indicates the swelling after mounting.

As linear correlations were seen among the points in both figures, the regression equations were calculated by the least square method. In Fig. 2 for Neo-Shigaral solution, the equation was

$$y = 1.02\,x + 0.002 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

, where y and x are the body lengths before and after mounting, respectively. The trend line is biased a little to the left of the equivalent line. The constant, 0.002, is so negligible that the equation can conveniently be expressd as $y = 1.02x$. Therefore the body length of Collembola tended to shrink a little in Neo-Shigaral solution. In Fig. 3 for Hoyer's solution, the equation was

$$y = 0.95x - 0.007 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

,where y and x have the same meaning as in Fig. 2. Contrary to the case of Neo-Shigaral solution, the trend line is biased to the right. The constant, 0.007, is again so negligible that the equation can be given as $y = 0.95x$. Consequently the body length of Collembola showed a tendency to expand in Hoyer's solution. If the body lengths of materials mounted in microscopic

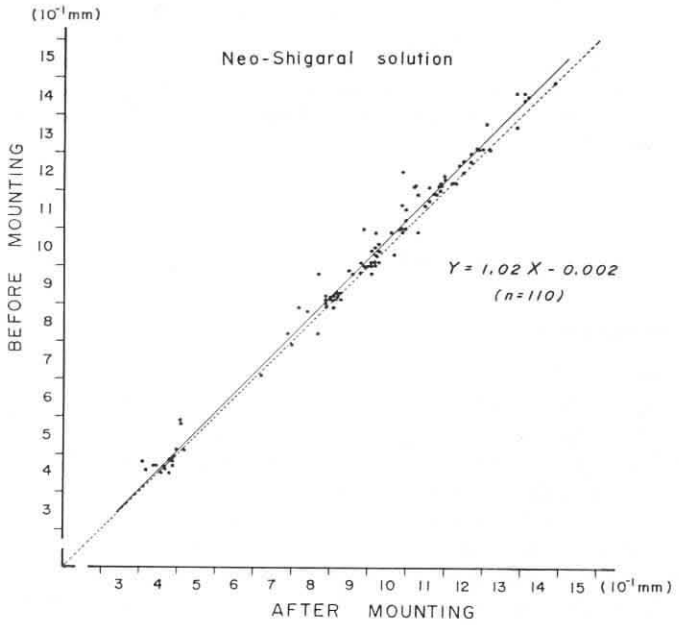

FIG. 2. — Effect of Neo-Shigaral solution on body length of *Folsomia octoculata*.

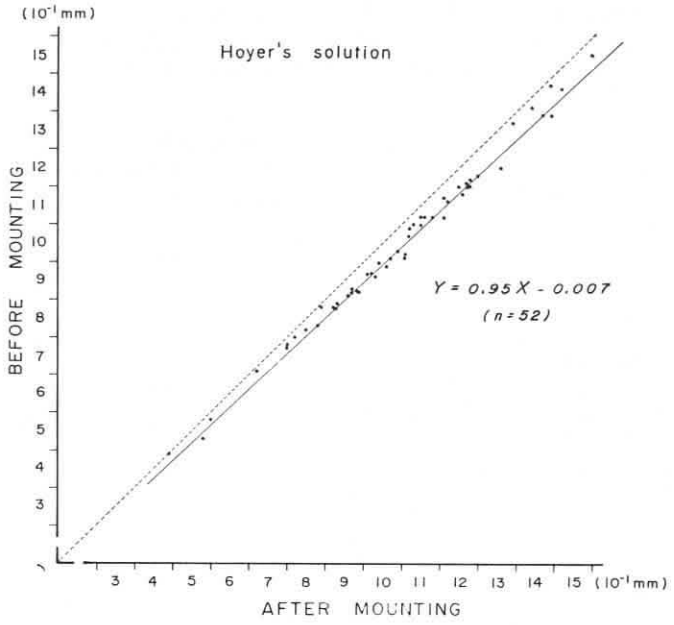

FIG. 3. — Effect of Hoyer's solution on body length of *Folsomia octoculata*.

preparations are measureed and the values are adopted in the equations (1) and (2), then natural * lengths of the specimens are obtainable.

In Neo-Shigarel solution, the deviations of points from the regression line are relatively large. Twenty four within a hundred and ten points (ca. 22 %) were distributed to the right of the equivalent line, these animals having indeed swollen in this medium. Therefore, the effects of Neo-Shigaral solution are unstable. On the other hand, in Hoyer's solution, the bodies of collembolan specimens expand with relatively large departures from the equivalent line. However, the deviations from the regression line were small. There was no point to the left of the equivalent line. This means that no individuals shrank in this medium. Therefore, the effects of Hoyer's solution are stable.

B. **Population composition.**

The corrected data are shown in Fig. 4 as frequency distributions of each size class, together with the original data. In comparison with the original data, all « natural populations » are composed of considerably larger number of individuals, but the patterns of population compositions are similar with each other. However, in the « natural populations » the patterns are much more emphasized. All the following descriptions are to be put forward upon the basis of the « natural population ». Therefore the term population means henceforth « natural population » unless otherwise mentioned.

The population of *Folsomia octoculata* ranges between 0.3 mm and 1.6 mm size class in body length, and all size classes are always found in the population, except from early winter (November) to early summer (July), during which the smallest classes (1st size class or 1st and 2nd together, in the terms of 0.05 mm interval size class) are absent. SHARMA and KEVAN (1963) measured the body length for individuals of a related species, *Folsomia similis* Bagnall, in culture as a straight line using eye-piece micrometer and gave 0.32 mm and 1.45 mm for the minimum and maximum sizes, respectively. Their results agree well with that of the present study except for a slight difference in the maximum size. Studies by NIIJIMA (1971) and TAKEDA (1973) on *F. octoculata* did not give precise values of the minimum and maximum sizes but reported the existence of individuals smaller and larger than 0.5 mm and 1.2 mm, respectively, both by using eye-piece micrometer under a stereoscopic microscope to measure the body length. Putting all data together, the size range obtained in this study appears to resemble that in other studies, though slightly larger in the maximum-sized individuals than that in other lower altitudes.

C. **Breeding period.**

The omission of the minimum size class in a given population means the absence of recruitment. Such omission, seen every year during November to July as mentioned above, is probably an outcome of a slight growth of the

* Effect of preservation medium, alcohol in this case, is ignored here, for its evaluation is hard at present, but the effect is believed to be not so severe as that of mounting medium.

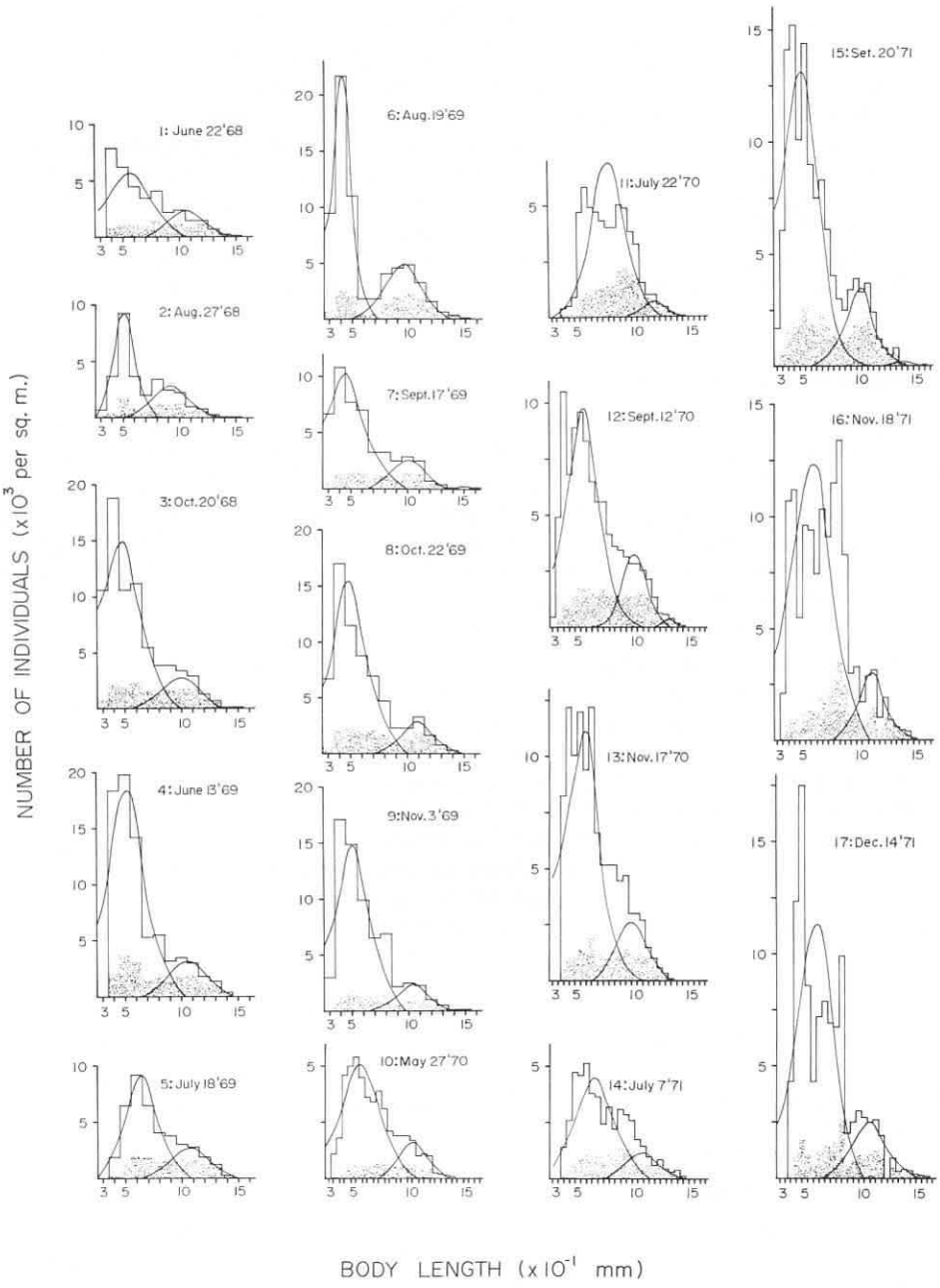

FIG. 4. — Frequency distributions of individuals for each size class together with normal curves calculated by Cassie's method (see text); dotted area corresponds to original uncorrected data.

recruited individuals without subsequent recruitments. In other words, recruitment occurred only from August to October. But this period does not directly correspond with the breeding period itself. In this oviparous animals the incubation period of eggs laid needs to be assessed in order to get the exact breeding period. However, the direct observation of eggs is impossible under natural conditions because the eggs are nimute and are never extracted with Tullgren funnels. SHARMA and KEVAN (1963), using a cultured population of *F. similis*, reported that the incubation period was temperature dependent, lasting 12-13 days at 17° C and 27-35 days at 11° C. Further, MARSALL and KEVAN (1962) observed a 18-20 days incubation period at 16° C in the rearing materials of another congeneric species, *Folsomia candida* Willem. MARSHALL and KEVAN's data are properly included within the range given by SHARMA and KEVAN both in temperature to which exposed and days required. From Fig. 4, the begining of recruitment is supposed to occur around August 1 because the recruitment does not yet appear on July 18, 1969, July 22, 1970, and July 7, 1971 but had already begun on August 27, 1969, and August 19, 1969, when maximum size of newly recruited individuals already attained at least 0.7 or 0.6 mm size classes. The incubation period aroung August 1, the hottest period throughout the year at the study area recording 15-17° C (Fig. 1), is possibly at least 15-20 days. The beginning of the breeding period in the present population must have occurred at least half a month before August 1, when the first recruitment appeared. These assumptions also may be applied to the determination of the end of breeding period. The breeding period had already finished at least half a month before November 5, when the first absence of the minimum size class individuals occurred. Consequently the breeding period of the population is guessed as starting in mid-July and ceasing in mid-October.

D. **Generation structure.**

Frequency distributions given in Fig. 4 have always one or two breaks, which separate the population into two or three different components. The most distinct example is seen in August populations. In 1968, August 27 population can be divided roughly into two groups by a drop at 0.7 mm. On the other hand, June 22 population lacks the smallest size class. The small-sized peak in August is thus considered to be the new generation composed of individuals recruited in the summer from mid-July to mid-August. Similarly, in 1969, the August 19 population can be divided into two components at 0.6-0.7 mm. The small-sized peak is also the new generation because the July 18 population had still no new recruitments. On the other hand, the large-sized peak is considered to correspond to the old generation born in the previous years and overwintered once or twice. Therefore each component bounded by the drops represents a generation. Provided that each component of the histogram separated by the drop represents a normal distribution of size classes, each cohort can be simply approximated by a normal curve composed of the same number of individuals with the corresponding unit of histogram. To separate a bimodal distribution into two normal distributions, Cassie's method (1954) using probability paper was employed. The results of these analyses are also given on the histograms in Fig. 4 as normal curves. In 1968, on June 22 the population was composed of two generations

without individuals of the minimum size class. On August 27 the recruitment of small individuals had already begun, and the large individuals from a small isolated cohort, suggesting three cohorts different in the year of birth from each other. Recruitment was continued at least till October 20, when the populations was composed of only two generations, by the disappearance of the oldest generation in August. In 1969, the population structure on June 13 was completely the same with that on October 20 in the last year except the absence of minimum size class. It suggests that no replacement of generations happened during the period between the two dates, *i. e.* in winter. On July 18 the generation composition was still the same. But on August 19 the new generation abruptly appeared having already a large number of individuals, resulting in the occurrence of three generations, with the oldest generation being imperceptibly decreasing and the smallest one markedly increasing in number. On October 22 only two generations were seen and the oldest one in September had already disappeared. On November 3 the population structure was almost the same as in October but the recruitment had nearly stopped judging from the scarcity of the minimum size class. In 1970, May 27 population was composed of two overwintered generations devoid of the minimum size class. On July 22 the generation composition was still identical with that in May without recruitment, while the dearth of individuals in small-sized classes was conspicuous. On September 12 new recruitment had already started with the overwhelming dominance of a new generation which coexisted with two other generations though the oldest one was scarce in number. November 17 population involved only two generations with extinction of the oldest one in September; recruitment had previously ceased. In the last year surveyed, 1971, the July 7 population was completely the same as that of the last November in generation composition. On September 20 the new recruitment was nearly completed. Among three coexisting generations the oldest one, however, had nearly disappeared from the population. The November 18 and December 14 population structures were similar to each other, but the shortage of individuals in minimum sized classes was more distinct in the latter.

Consequently the generation composition of the population is seasonally different but stable year by year. In other words, the generation composition at a given season can be expected to be the same as those at the corresponding season of different years. In conclusion, each generation of the population studied appears to require a little more than two years from birth to extinction. Therefore during the four years' survey, six generations occurred of which two, recruited in 1968 and 1969, completely passed their lives from start to end during the survey as shown in detail in the next section. The recruitment period is short, from early August to late October (cf. V-C). Most recruitment occurs from early August to late September, during which most parts of the generation alternation is also completed; and the most dynamic phase of population change occurs during August.

E. **Growth analysis.**

As seen in Fig. 4. one unit of the histogram set off from other units by low values corresponds to a generation which can be properly approximated by a normal distribution. The modal value means the representative body

size of the generation concerned at any time. When the modal size is plotted against time, the resulting graph may demonstrate the growth pattern of a representative individual in a given generation under natural conditions. In Fig. 5 the theoretical average growth curve was prepared by smooth tracing by eye of the plots of modal size. The upper and lower limits of the variation range, similarly traced from the amplitude of standard deviations, may cover most individuals belonging to the same assemblage.

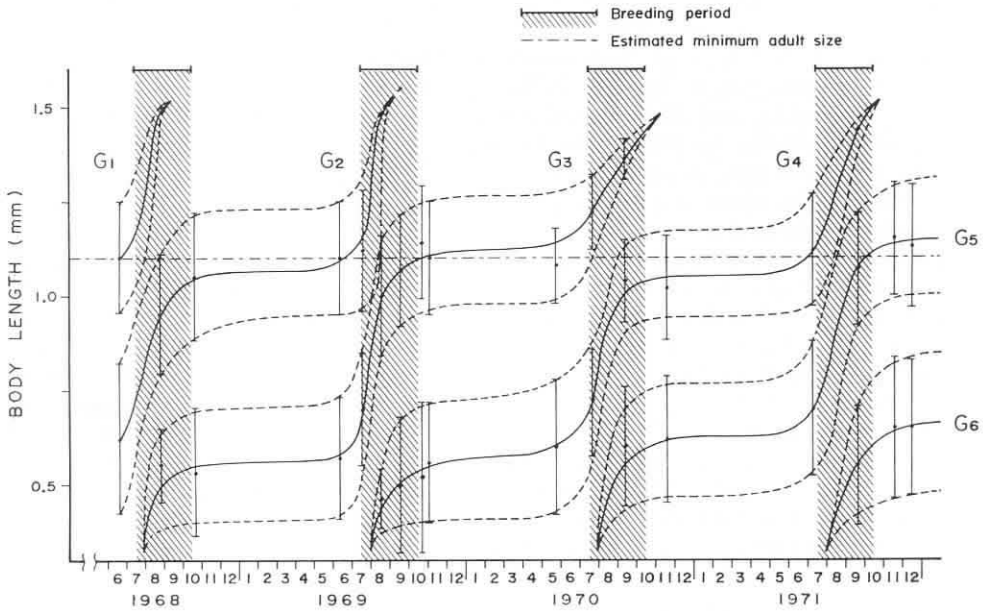

FIG. 5. — Theoretical growth curve based on size class for each generation (G_1) during 1968-1971; vertical bars indicate standard deviations.

Six generations which occurred during these four years were symbolized as G_1 - G_6 in sequence order. The G_1 had already passed through the second overwintering period in its life by late June in 1968. Then it attained the adult stage with the body length more than 1.1 mm, applying the result by SHARMA and KEVAN (1963) who gave 1.10-1.45 mm as adult body length for a related species, *Folsomia similis*. It abruptly grew during the warmer season and disappeared from the population by early October. The G_2 had overwintered once and was still immature in late June in 1968. It also rapidly grew during the warmer months, some large individuals exceeding 1.1 mm in late September taking into account the standard deviation. Therefore a fraction of the individuals might breed during the latter half of the breeding period, though the theoretical average individual (1.00-1.05 mm in size) was still subadult. But, at the lowest estimate, two thirds of the generation appeared to delay breeding till the next year. The G_3 newly recruited in early August in 1968 seemed to be more or less 0.33 mm in body length. It showed a slight increase in size in the course of the first growth period and stopped

growing at the level of about 0.55 mm by early November with the onset of the cold season; thereafter it passed through the winter without growing. The second growth started in May with the partial liberation from snow cover. A complete exposure of the forest floor accelerated the growth of individuals which reached an average length of 1.1 mm in October. Taking the standard deviation into consideration, some large individuals seemed to start breeding in mid-August. But at least half of the individuals apparently delayed breeding until the next season. The individuals stopped their growth by early November and entered into the second overwintering at the level of about 1.12 mm in size. The G_3 released from the second dormancy began again to increase in size and totally maturated by the begining of second breeding season (early August, 1970). Cooperating with some individuals of G_4 it produced G_5 and disappeared from the population at ca. 1.5 mm in length by early November in 1970. The G_4 recuited mainly by the G_2 and partly by the G_3 appeared first in early August with the size about 0.33 mm, and attained about 0.57 mm, when it entered into the first overwintering. Posthibernation individuals showed a sudden increase in body size to attain 1.05 mm before the second overwintering. During the course of the second growth period, one fourth or one third of the G_4 might mature, but most individuals did not participate in reproduction till the next warm season after the second dormancy. At the beginning of the second breeding period all individuals became ripe and continued to produce at G_6 till extinction in early November in 1971. The G_5 born in early August in 1970 at once started to grow, but ceased growing at ca. 0.52 mm with the onset of winter in mid-November. The dormant state continued for about six months till start of growth in the next mid-May. Since mid-November the G_5 entered into the second dormancy probably till next mid-May. The G_6 began to grow with incorporation into the population in early August in 1971, but soon began overwintering possibly till the release from dormancy in the next mid-May.

Combining all information, a given generation recuited in summer passes through three growth periods and overwinters twice until the disappearance at the end of autumn two years later. The individual born at ca. 0.33 mm became a little less than twice as large in terms of body length during the first growth period, more than three times the initial size during the second period and nearly 4.5 times by extinction after passing through the third growth period. Judging from Fig. 1, the growth in the study area seems to occur at air temperatures over 5° C, which is regarded as the critical thermal limit to the growth of *F. octoculata*.

The growth rate in terms of body length of each generation was obtained (Fig. 6) directly by reading the size increment for every 15 days from Fig. 5. Reflecting sigmoidal nature of growth curves in Fig. 5, the seasonal trend of growth rate for every generation showed the normal distribution in the growth period, virtually concentrated in July and August with the peak in August every year. As shown in Fig. 1, these months, especially August, have always the highest monthly air temperature (15-17° C) throughout the year. The maximum growth rate per 15 days for each generation was as follows: 0.175 mm in G_1; 0.190 mm in G_2; 0.170 mm in G_3; 0.125 mm in G_4; 0.115 mm in G_5; and 0.072 mm in G_6, most in early August, though the last two generations were not observed through their full life cycle. Assuming the maximum

growth rate per 15 days tentatively as 0.17 mm, about 14.5 % of the total growth is acquired during the first half of August because the minimum size is 0.33 mm and the full size 1.50 mm in the theoretical curve in Fig. 5. Therefore a generation of *F. octoculata* seems to require theoretically about 103 days

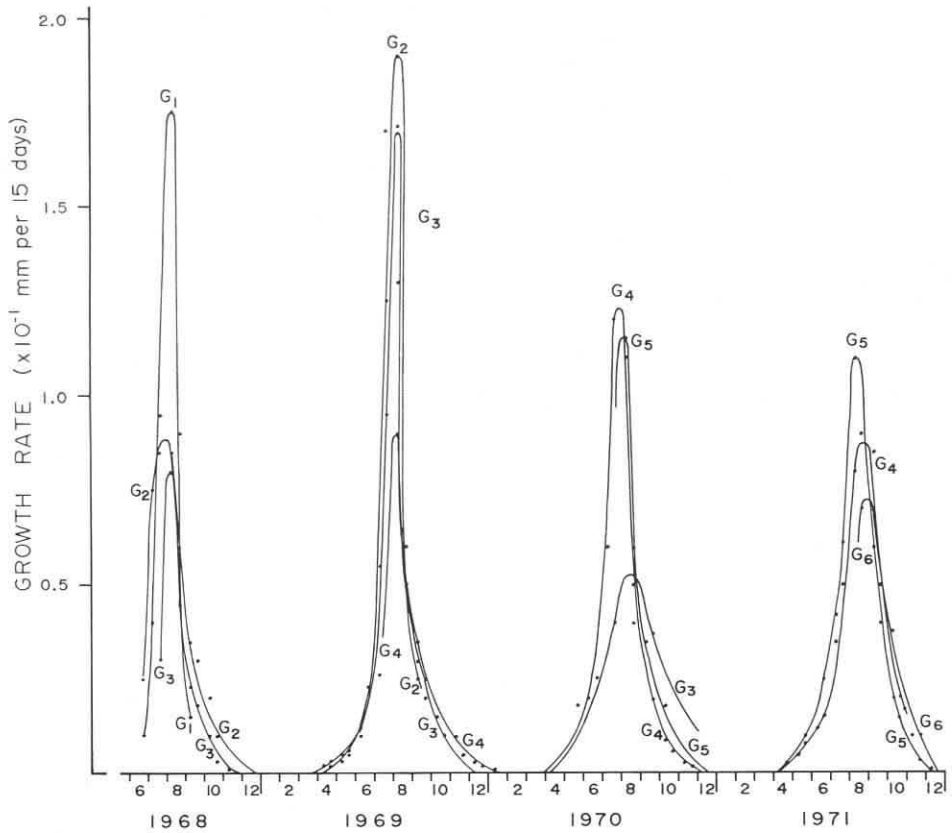

FIG. 6. — Seasonal change of growth rate (mm/15 days) for each generation during 1968-1971.

to complete its life cycle, if it is laid under experimental condition with constant temperature corresponding to the mean air temperature (16.0° C) in early August in the surveyed area. Unfortunately data from culture of *F. octoculata* have never been reported. This estimation, however, agrees relatively well with the result from the experimental population of *F. candida* by SNIDER (1973) who reported the mean longevity of 136 days at 15° C constant temperature. Consequently it is inferred that the long life span of the population studied is mainly caused by the long inactive period covering three fourths of the year in the area surveyed.

F. **Population dynamics.**

1. Outline in terms of the total number of individuals.

Seasonal change of the corrected total density of the population during four years is presented in Fig. 7, together with the uncorrected original data. The pattern of population fluctuation is quite irregular depending upon the year. However, a trend common to each year is noticeable. A large depres-

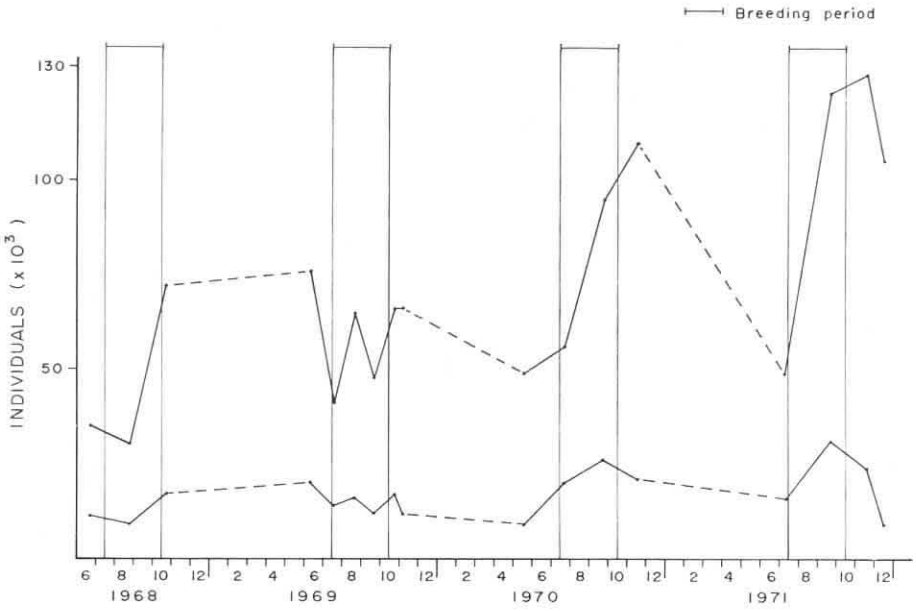

FIG. 7. — Seasonal change of total numbers of individuals, both corrected (upper curve) and uncorrected, during 1968-1971.

sion occurs every year in summer mostly, details being as follows: August (1968), July (1969), May (1970), and July (1971). In the case of 1968, July population, if sampled, might have the minimum density in the year. July population in 1970 might be overestimated by sampling bias because the new recruitment had not yet begun. Combining all data together, it is suggested that the population has the minimum density just before the beginning of each recruitment (July), followed by a rapid increase during the breeding period till early November, then gradually decreases toward the next July through winter. The maximum density ranged between 65,000 and 130,000 individuals per sq. m but was quite different every year, the peak in 1971 being twice as high as in 1969. The population density showed a steady increase for four years concerned except for a slight decrease in 1969.

The original uncorrected data exhibit a seasonal pattern similar to the corrected ones, but there is a decisive difference between them in density. Examining both graphs (corrected and uncorrected) in detail, the following slight discrepancies are recognized: (1) reversed amplitude of two declines

in July and September, 1969; (2) disappearance in the corrected data of a drop in November compared with October, 1969, in the original data; and (3) increase in November, 1970 and 1971 in the corrected data, in contrast to decrease in the original data. Allowing for some insufficiencies, the direct analysis of original data may help to apprehend an approximate fluctuation pattern, but is dangerous to use for estimation of various population parameters.

2. Analysis in terms of generations.

The actual number of individuals sampled may over- or underestimate the real density depending upon the sampling time due, perhaps, to sampling biases. These biases, if any, must be corrected. But the absolute correction for a single sampling time is impossible here. An approximation was thus unavoidable, where the most plausible trend line was drawn by eye through the actual values. However, it is difficult to determine wheter such a trend line is the best approximation as far as the total population is used, for the total population consists of components, each of which behaves rather independently. Consequently at first the total population must be divided into its components, or generations. By separately tracing the densities of each generation with time and then cumulating them, the population fluctuation can be systematically analysed. The number of individuals belonging to each generation at each sampling data is given also in Fig. 4 as a quantity expressed by a normal curve. The overlapping area includes individuals of both generations. These numbers were plotted against the sampling data in Fig. 8. These plots showed large fluctuations in each generation as if there were no trends. This seems to have been caused by the sampling error. However, this can be corrected on the following basis: (1) during the breeding period, a new generation will continue to increase in number unless there is a high mortality; and (2) after the breeding period, the generation will continue to decrease in number, due to the mortality factors, till all members disappear from the population. On such considerations, a smooth trend curve was drawn by eye through the plots of density against time for each generation. These results were also shown in Fig. 8 as smooth curves.

At the first sampling time, June 22, 1968, G_1 and G_2 were already in the state of decreasing phase. G_1 disappeared by late September of the year, while G_3 was incorporated into the population in early August. G_2 also became extinct by late September in 1969 after the second overwintering, replaced by the G_4. G_3 steeply increased in number till the peak (61,000 per sq. m) in early November. With the onset of winter it stopped increasing and entered into the decreasing phase. The decreasing phase may be largely divided into four periods as follows: (1) *First decreasing period*, nearly corresponding to the first overwintering period, during which the generation shows gradual decrease perhaps due to natural death alone because of the lack of predation, when the predators such as centipedes, spiders, prostigmatid mites, etc. are in the state of dormancy under the snow cover; (2) *Second decreasing phase*, being equal to the second growth period mentioned in V-E, during which the generation abruptly dwindles presumably due to increased predation after winter dormancy; (3) *Third decreasing period*, which is the repetition of the first decreasing period; and (4) *Extinction period*, which is the repetition of

the second decreasing period during which the post-reproductive senility, too, may be one of the main causes of the rapid decrease, adding to the predation. For example, G_3 changed in the density per sq. m at the end of each period as follows: 50,000 (1); 10,000 (2); 7,000 (3); and null (4) and G_4 from 58,000 (increasing phase (i.p.)) to 45,000 (1); 19,000 (2), 11,000 (3); and null (4). G_5

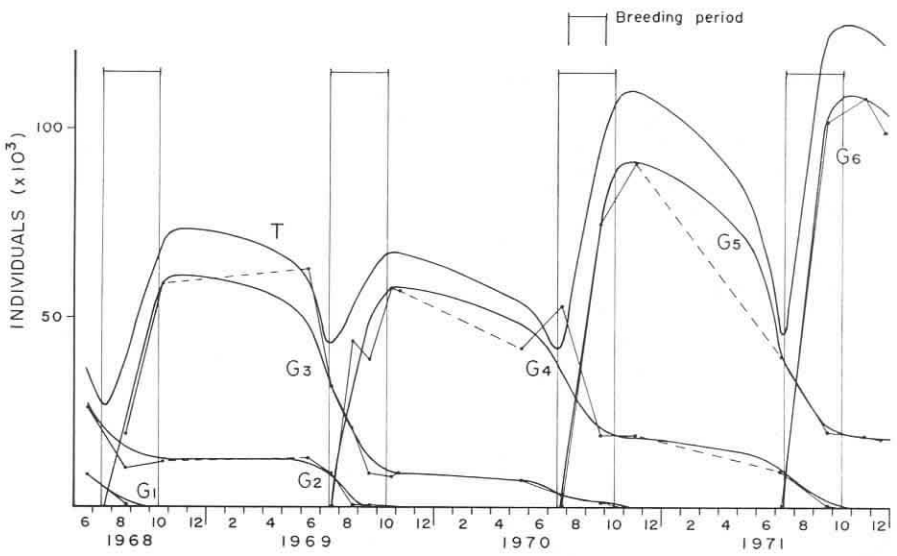

FIG. 8. — Seasonal change of density for total population and each generation during 1968-1971. Dotted part of line means period without sampling. $G_{(1-5)}$ are lines smoothed by eye. T is total population based on the sum of values for each of the generations.

decreased as follows: 91,000 (i.p.); 70,000 (1); and 20,000 (2). G_6 had a density of 109,000 (i.p.), but the subsequent change was unexamined because of interruption of the survey. Combining data of G_3 and G_4 which completely finished the life cycles within the survey period, the relative change of a generation may be approximately summarized. Regarding the peak at the end of increasing phase as 100, each decresing period is responsible for the disappearance of the generation in terms of the decrease relative to the maximum density as follows: 20 % (1); 63 % (2); 5 % (3) and 12 % (4).

Next, the total population density was estimated by cumulating the values of each generation at a given time, as shown in Fig. 8. Examination reveals that the corrected curve of total density fits fairly well the actual curve (cf. Fig. 7). This four years' fluctuation is a repeated series of a unit, its fundamental structure being a set of the peak at the end of breeding period and the drop just before the breeding period. The maximum densities per sq. m in each year were 73,000 individuals (1968), 67,000 (1969), 110,000 (1970) and 128,00 (1971). As described in V-F-1, the population density tended to increase gradually with a slight drop in 1969. But the causes responsible for such a phenomenon are unknown at present; they cannot be explained by the climatic conditions alone, which were not particularly different among four years.

VI. — DISCUSSION

A. Population structure and life span.

The studied population of *Folsomia octoculata* is complicated by the coexistence of three cohorts in a breeding season and of two in a non-breeding period. Each cohort is respectively regraded as the independent generation different in the year recuited, judging from its annually stable pattern in rise and fall and from a regular lack of the minimum size classes in overwintering periods. Each generation is always recruited in mid-summer and lives by early autumn two years after passing through two winters. Therefore generations coexisting at a given time are exposed to the same environmental conditions at the nearly same developmental stage. This sharply contrasts with polyvoltine species with overlapping generations, e. g. *Isotoma trispinata* with six generations per year in Kyushu, Japan, (TANAKA, 1970 b) in wich each generation experiences seasonally particular environment at different developmental stages. The population studied in this paper is, in a sense, rather easy to analyse. The population can be simplified to be a cumulation of generations with identical ecological quality, though there being probable annual differences, enabling a general comprehension of the population by intensive study on a generation. Newly recuited individuals (ca. 0.33 mm in body length) belonging to a particular generation immediately grow rapidly during the first growth period lasting three months from early August to early November. From the theoretical growth curve, the generation becomes a little less than 2 times larger (ca. 0.57 mm in body length) than the initial size during the period, the growth rate during which is 0.033 mm per day in average, more than 3 times (ca. 1.08 mm in size) during the second period and nearly 4.5 times (ca. 1.50 mm in actual size) during the third period followed by the extinction from the population. At its extinction, other generations recruited in the subsequent two years had already been incorporated into the population. Between these three growth periods, two long overwintering periods are inserted, during which the animals are dormant without growth. The long overwintering may be responsible for the prolonged life span. The longevity is surely temperature dependent (SNIDER and BUTCHER, 1973). In general, lower temperature lengthens development time, while higher temperatures act oppositely (BUTCHER et *al.*, 1971). But superoptimal temperatures must decrease the development, becoming lethal (THIBAUD, 1967; 1968). Collembola are relatively resistant to low temperature and can live in frozen soil (TAMURA et *al.*, 1969) though with considerable delay of development (BUTCHER et *al.*, 1971). The life span of this subalpine population (ca. 750 days/life) looks extremely long compared with those of *F. candida* which takes in cultured condition 230 days at 25° C (GREEN, 1964) and 240 days at 15° C (SNIDER and BUTCHER, 1973). NIIJIMA (1973) reported 255 days' life span at 15° C for *Sinella curviseta* and observed a few individuals survived for about 1.5 years (corresponding to ca. 550 days) at 15° C. Therefore the life span estimated in the present study is reasonable. Subtracting the duration of two dormant periods (ca. 420 days) from the life span, the difference of 330 days is obtained. Mean air temperature during growth period (mid-May to mid-October) is 11.3° C. Considering this value, the length of the life span may not be surprising.

B. Breeding.

The breeding period of this population begins in mid-July and stops in mid-October every year. Individuals over 1.1 mm in body length are regarded as sexually mature adults. Assuming sex ratio is 1:1. one half of individuals

over 1.1 mm at a given time within the breeding period are regarded as adult females capable of oviposition. From Fig. 5, a generation has two breeding periods during its life. At the first breeding period only part of the generation matures; possibly these are the individuals born in the beginning of the last breeding period. However, at the second breeding period, all surviving individuals mature. Thus two successive generations are responsible for reproduction in a given breeding period. Such a reproductive pattern has never been reported in Collembola, but in a leech, *Glossiphonia complanata* (L.), inhabiting a tributary of the River Pang, Berkshire (MANN, 1959). The leeches breed for the first time at one year age, and for a second time at two years age. At a given breeding period only 40 % of one year old leeches reach maturity, while 100 % of two year old leeches breed and most die soon after. Mann analysed the result on the basis of confirming clitellum for maturity and eggs or young carried attached to the ventral surface of adults for breeding. In the present study, the breeding of the population as a whole was recognized by the occurrence of new recruitment but maturity was not confirmed because of the lack of diagnostic characters for adult in most collembolan species. Since information about the maturity is lacking, a refined picture of the entire life history can not be drawn. Unfortunately cultured populations of the present species have never been successful because its strong thigmotactic nature makes the culture on the flat substratum in a glass jar, which is convenient for observation, impossible (NIIJIMA, personal communication). The most reliable means for determining maturity is a direct observation of gonads, especially ovries, of collembolan individuals. So the exploitation and refinement of such methods are desired for further development of this study.

C. **Population dynamics.**

The population studied had six generations within the four years, each behaving independently. Closer analysis revealed the presence of two or three generations at a given time depending upon seasons. From birth till removal from the population by death, each generation changes in the number of individuals, and the population fluctuation is the composite of the fluctuations of these two or three generations. The amplitude of the fluctuations is determined by the extent to which the generations are affected by the environmental conditions. The population fluctuation during the four years is fundamentally composed of a peak and a drop one by one per year. Each peak-drop set is as follows: 73,000-26,000 individuals per sq. m (1968), 67,000-43,000 (1969), 110,000-42,000 (1970), and 128,000-45,000 (1971).

It is generally considered that the total density of Collembola per sq. m ranges 10^4-10^5 individuals in various habitat types (for details see HALE, 1967; WALLWORK, 1970). But, as mentioned just above, *F. octoculata* population showed remarkably high densitites. This conspicuous difference was undoubtedly introduced by the correction. Applying a simple correction to the whole collembolan assemblage of this study area, by multiplying the density of *F. octoculata* by 2.5, the total density becomes 182,500-65,000 (1968), 167,500-107,500 (1969), 275,000-105,000 (1970), and 320,000-112,500 (1971), for 40 % of the assemblage was made up of *F. octoculata*. Consequently hitherto reported information on the densities of Collembola may be more or less underes-

timated. When these data are intensively corrected, e.g. along the present procedure, each local density may exceed the order of 10^5 individuals per sq. m. This is supported by TAKEDA (1973), in which he reported that partially corrected density of *F. octoculata* in Kyoto, Japan, exceeds 10^5 per sq. m. throughout the year. This is the only work so far published on more or less corrected densities.

As far as the surveys on Collembola hitherto reported are concerned, most of them have severe defects in the evaluation of rather small-sized individuals. Using the data obtained in this study, this affair is explained as follows. Examination of the original data of the population structures shown as dotted area in Fig. 4 (Nos. 3, 8, 9, 13, 16 and 17; all in October, November and December, when the recruitment was almost or completely finished) reveals that the younger generation has the number of individuals a little over or almost equal to that of the older one. In other words, the younger generation loses few individuals till that time in the next year, though provided year to year deviations are ignored. This gives an important objection to the traditional opinion regarding Collembola as a land plankton. If this opinion is true, a fairly large quantity of individuals must be lost not only by natural death but also by predation during the life span. On the other hand, the corrected pictures well agree with the traditional opinion, for the younger generation possesses a large enough stock of individuals to satisfy the predators till they become the older generation one year after.

D. **Reproduction program.**

The life history of the population studied is schematized as shown in Fig. 9. But there is an important weakness in the figure, which is attributed to the lack of actual data for the maturity of females. In this study, *F. octoculata* was assumed to be mature at over 1.1 mm in body length, following to SHARMA and KEVAN (1963). In this study, it is in September, one year after birth, that a portion of a given generation first exceeds 1.1 mm in body length, even in reference to the standard deviation in the cohort (cf. Fig. 5), when the air temperature at the study area is about 12-13° C and rapidly declining since August. However, if the collembolan populations are adapted to the environmental conditions lived in, it is not impossible to suppose that they entirely reserve their breeding capacity till the next favorable season, though there are virtually no data on such adaptive programs to the climatic change in Collembola. Concerning the population studied there are three possible reproductive programs: 1) the individuals of the generation begin to reproduce within the year of birth; 2) some individuals commence breeding one year after birth, but most two years after; and 3) all individuals breed first two years after birth. 1) is the least possible because in their first year even the largest individuals, judging from the standard deviation in Fig. 5, do not attain the length presumed to be characteristic of maturity. 2) is the most possible (for details see text). 3) is also possible. In the last case the generation only breeds two years after recruitment. At this time other generations have not yet attain marurity. Therefore a single generation is alone responsible for the breeding in a given year. This type of life cycle can be schematized as in Fig. 10. There the population has two independent reproductive sequences, viz. $G_{n-2} \rightarrow G_n \rightarrow G_{n+2} \rightarrow$ and $G_{n-1} \rightarrow G_{n+1} \rightarrow G_{n+3} \rightarrow$. Even if it can not

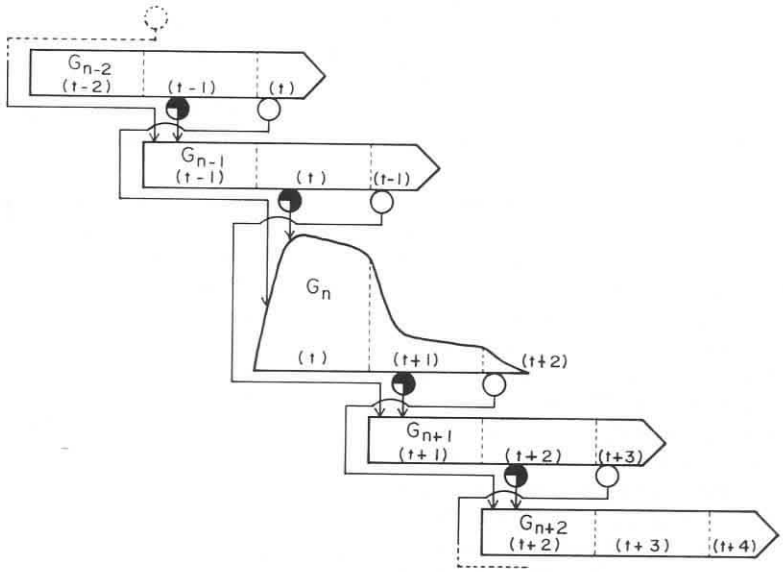

FIG. 9. — Schematized life cycle of G_n-generation, together with preceding and following generations in reproductive sequence, in the case of two breeding periods in life cycle. G_i: generation i; t_i: time passed in year by G_i; circle: abbreviated age structure in females; black sector: immatures; white sector: matures; and arrows: reproduction.

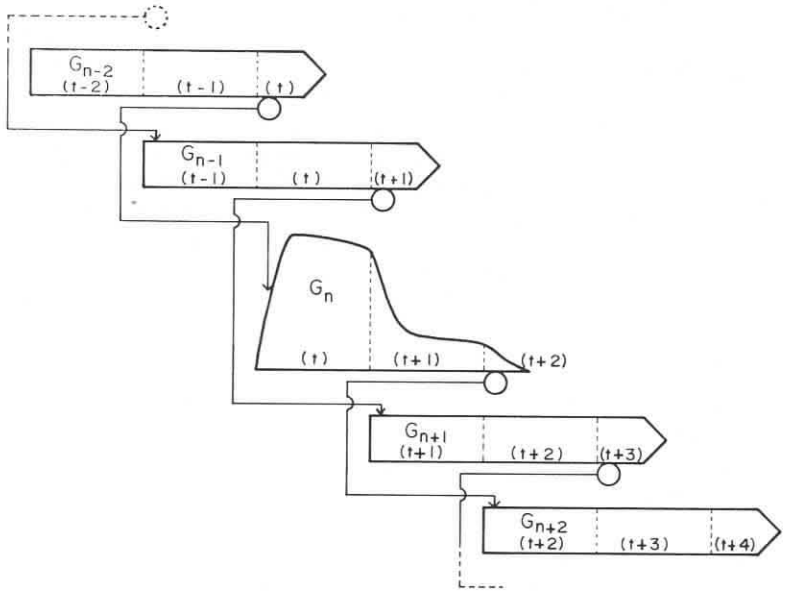

FIG. 10. — Schematized life cycle of G_n-generation, together with other generations with reproductive sequence, in the case of single breeding in its life. Further explanation as in Fig. 9.

happen in the present study area, this type of life cycle may occur in the districts more severe in climatic conditions, for the reduced warmer season may make the breeding shift entirely to two years after recruitment. Consequently at present, 2) is the most plausible as the explanation for the present population. However, the possibility of 3) remains till it is denied, for such an instance appears to be actually seen in a Wilfin Beck population of the leech, *Erpobdella octoculata* (L.) (ELLIOT, 1973). For the solution of these problems, direct observations of the ovarian development of collembolans periodically sampled from the field are required.

SUMMARY

This study was carried out in order to get a « real » population dynamics of *Folsomia octoculata*, the most dominant species in Shiga Heights during 1968-1971, by adopting the improved estimation techniques. The area surveyed is in the subalpine coniferous forest with an annual mean air temperature of ca. 3.7° C, with soil type mostly wet podsol. Sampling was made 17 times during the four years to cover various seasons.

Individuals of the population range between 0.3 mm and 1.6 mm in body length and the population is always composed of two or three generations differeing in the year born. The breeding period appears to begin in mid-July and to end in mid-Octobor. The population structure is seasonally different but stable year by year. Each generation appears to require a little more than two years from birth to extinction. Six generations occured during four survey years. Theoretically an individual born at 0.33 mm becomes about 2 times as large in body length during the first growth period and nearly 4.5 times at extinction. The peak of growth rate is seen in August every year. In terms of total number of individuals, the population exhibits a similar population trend to that of the original uncorrected data, but there is a decisive difference in density between them. For each generation, fluctuation was corrected into smooth curves (for details see text). The total number of indiduals of the population is obtained by cumulating respective individuals of every generation existing at a given time. The maximum density per sq. m of the population is seen at the end of the breeding period every year, as follows: 73,000 (1968), 67,000 (1969), 110,000 (1970), and 128,000 (1971). A gradual increase in density was observed except for slight decrease in 1969.

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